



Synchrotron computer tomographic (CT) scans complement traditional techniques in understanding the internal anatomy of permineralised *Fontainocarpa* (Crotonoideae, Euphorbiaceae) fruits from the Oligocene of eastern Australia



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ABSTRACT

The internal morphology and anatomy of silicified fruits of *Fontainocarpa* were studied using traditional thin sectioning techniques, SEM and synchrotron computed tomographic (CT) imaging and animations, to enable comparative analyses with extant, indehiscent-fruited genera in the Euphorbiaceae including *Fontainea*, *Aleurites* and *Hylandia* from Australia, and other non-Australian crotonoid genera. Thin sections and sectioning show that the fruits of *Fontainocarpa* are indehiscent, multicarpellate and usually 3- to 5-loculate, with axial placentation, a single ovule per carpel and the ovules are anatropous and have antitropous curvature. A ventral vascular trace that supplies each ovule is embedded in the bitegmic seed coat. The internal anatomy is therefore consistent with the Euphorbiaceae. Additional characters, including indehiscent fruits, distinctive vascular channels (foramina) that penetrate through the fruit wall into the locule, and thin membranous seed coats are restricted to very few genera in the Euphorbiaceae, but occur together in extant *Fontainea*. The seed coat in extant *Fontainea* and fossil *Fontainocarpa* seeds is membranous, and appears to lack the palisadal exotegmen of most genera in the Euphorbiaceae. *Fontainocarpa* fruits were compared with those of extant *Fontainea* and the fossil has a combination of features unlike those of extant taxa. It shares with *Fontainea picrosperma* in having endocarps with convex intersutural surfaces lacking ornamentation and a similar number of locules and with *Fontainea venosa* in having conspicuous foramina. This study therefore supports a close relationship between *Fontainea* and *Fontainocarpa* and is further evidence of the Crotonoideae in the fossil record in Australia, and is one of the few records of this subfamily worldwide. This study is one of the few, to date, using synchrotron CT imaging to reveal the internal morphology of silicified fruits and to utilize animations to examine the structure of these fruits.

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1. Introduction

Seeds and fruits from a silicified flora from near Capella, Central Queensland was shown to consist of a diverse assemblage of rainforest taxa (Rozefelds, 1990). One of the taxa described as a new genus of Euphorbiaceae, *Fontainocarpa*, was compared to the extant genus *Fontainea* which is one of the few genera in this family from Australia with indehiscent fruits. The original, although somewhat preliminary study, focused on external fruit structure and overall appearance of the fruits highlighting characters, such as fruit shape, presence of foramina in the indehiscent fruit wall, and variable number of locules.

Since the original study was undertaken molecular-based systematics (Tokuka, 2007; Wurdack et al., 2004, 2005) have provided greater clarity into relationships within the Euphorbiaceae. In addition other botanical studies particularly those on pollen (Erdtman, 1952; Punt, 1962; Köhler, 1965; Nowicke, 1994; Levin and Simpson, 1994; Simpson and Levin, 1994; Nowicke et al., 1998, 1999; Takahashi et al., 2000; Nowicke and Takahashi, 2002; Matamoro-Vidal et al., 2012) have contributed to a clearer understanding of relationships in the family (Webster, 2014) and also into others, including the Picrodendraceae, Putranjivaceae and Phyllanthaceae previously included in the Euphorbiaceae, but now recognized as distinct (Angiosperm Phylogeny Group IV, 2016).

There is also a scattered literature describing and illustrating ovule development, and fruit and seed morphology in the Euphorbiaceae (Wichmann, 1880; Gram, 1896; Mandl, 1926; Netolitzky, 1926;

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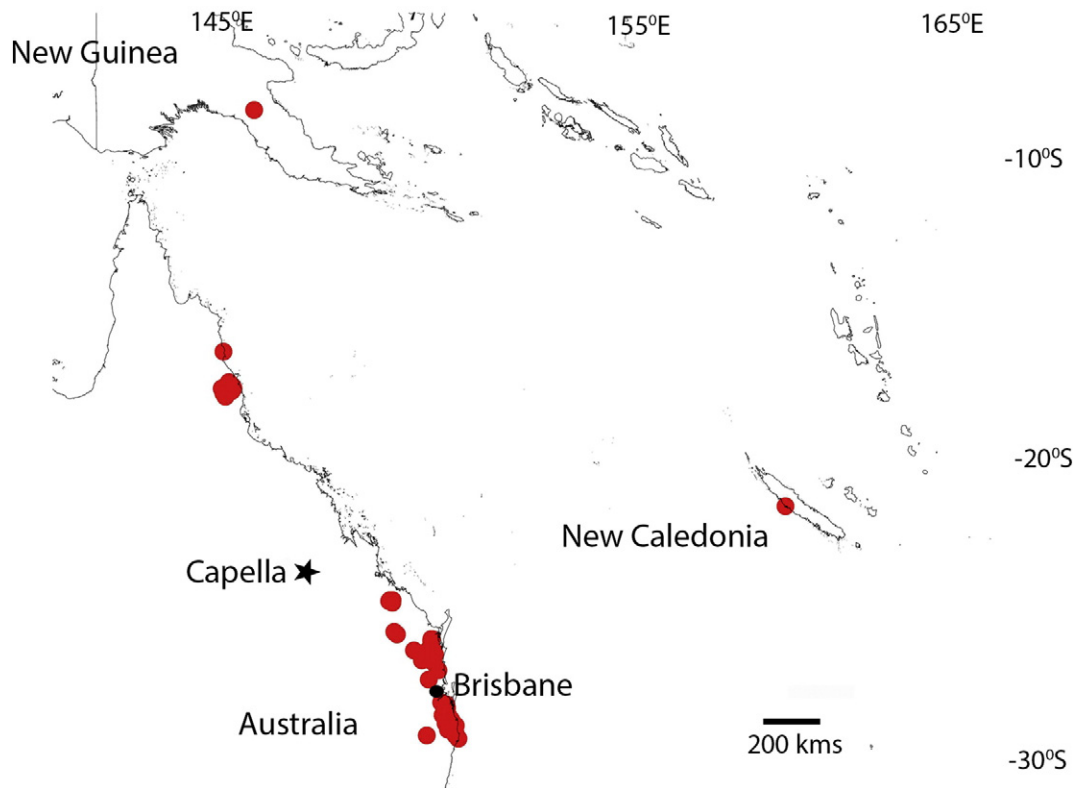


Fig. 1. Map showing the distribution of extant species of *Fontainea* based upon the *Atlas of Living Australia* records, and the fossil site near Capella.

Landes, 1946; Singh, 1954, 1968, 1970; Singh and Chopra, 1970; Wunderlich, 1968; Corner, 1976; Tokuoka and Tobe, 2003). More comprehensive and comparative studies on seed morphology have been

completed on the Crotonoideae (Tokuoka and Tobe, 1998; *Jatropha*, Dehgan and Webster, 1979), Euphorbioideae (Tokuoka and Tobe, 2002), and Picrodendraceae and Phyllanthaceae (Stuppy, 1996).

Plate I. 1. Volume render of extant *Fontainea pancheri* fruit showing the exocarp (Ex), mesocarp (Me), endocarp (En) and the walls of the endocarp which shows faint radial lines indicating the presence of foramina (F); there is a single developing seed (O) with a conspicuous seed coat (SC) and the position of the chalaza (C) is shown (BRIAQ 349534). 2–4. Extant *Fontainea venosa*, photographs of external appearance of fruit stone (endocarp), placement of seed in fruit and detail of surface of seed of *Fontainea venosa* endocarp (BRIAQ 633445). 2. Shows the ovoid shape of the endocarp, and conspicuous depressions of the foramina (F) in the endocarp wall. 3. The mature single seed is supplied by a ventrally placed vascular trace (VS) and the seed occupies a central position in the fruit and has expanded to fill the entire inner cavity of the fruit compressing the inner carpel walls, adjoining locules and soft tissues. 4. The seed showing the hilum (H), conspicuous ventrally placed raphe (R), nucellar beak (NB) and placental tissue (S). 5. Extant *Fontainea picrosperma* showing the prominent ridges in the endocarp, apical beak and single foramen (F) at terminus of each carpel. 6–10. Synchrotron images of *Fontainocarpa foraminata* (QMF16743). 6–7. Volume render showing the external appearance, prominent longitudinal lateral ridges, sutures (S) aligned along the longitudinal ridges, and conspicuous longitudinal placement of foramina (F) along the mid line of the intersutural surfaces of the endocarp. 8–10. Internal volume render of whole specimen showing the internal morphology of the endocarps. 8–9. Longitudinal view showing the arrangement of foramina (F) within the fruit wall, and two ovules (O). 10. Transverse view showing the placement of ovules within the fruit. Scale bar = 5 mm.

Plate II. Transverse section of *Fontainea venosa* fruit (BRIAQ 633445). 1. Section through fruit showing the fruit wall consisting of a light coloured layer of sclereids (Sc) and internal layer of tangentially oriented fibres (Fi), foramina in the intersutural surface and sutures (S) of which there are four, indicating that the fruit was originally 4-locular, with two seeds (O) and the narrow cavities and the carpel walls (CW) are evidence of two aborted ovules. Scale bar = 5 mm. 2. Detail of fruit wall showing the inner zone of tangentially arranged fibres (Fi), and carpel wall (CW), and suture (S). Scale bar = 1.25 mm. 3. Detail of carpel walls (CW) surrounding the two seeds (O), note the narrow seed coat (SC). Scale bar = 1 mm. 4. Detail of outer sclereids (Sc) and inner fibres (Fi). Scale bar = 500 µm. 5. SEM micrograph showing the external appearance, and outlines of the epidermal cells of the seed coat. Scale bar = 50 µm. 6. SEM micrograph showing irregular arrangement of sclereids in the fruit wall. Scale bar = 200 µm. 7. SEM micrograph of seed coat showing longitudinal section through the seed coat and radial alignment of cells of the testa. Scale bar = 50 µm. 8. Detail of 6, showing the regular pitting of the sclereids. Scale bar = 100 µm. (see on page 46)

Plate III. *Hylandia dockrillii* fruit (ATH QRS 500075) 1–2. Lateral and distal view of bilobed fruit showing the septicidal lateral sutures (S). Scale bar = 1 cm. 3–4. Transverse section and line drawing of the fruit, showing exocarp (Ex), loosely arranged fibres in the mesocarp (Me) and vascular bundles (vb) at the base of the mesocarp, thin carpel walls (CW), ventral vascular traces (VVT) and thick seed coat (SC). Scale bar = 1 cm. 5. SEM of fruit wall showing the loosely arranged fibres of the mesocarp (Me) and the outer exocarp (Ex). Scale bar = 500 µm. 6. Detail of 3, showing carpel wall (CW) and radially-arranged cells in seed coats and vascular bundles (vb) at the base of the fruit wall. Scale bar = 5 mm. 7. SEM of seed coat showing the radially-arranged, thickened columnar cells. Scale bar = 50 µm. (see on page 47)

Plate IV. Transverse sections of fossil fruits of *Fontainocarpa* and modern *Fontainea*. 1.2. *Fontainea venosa* (BRIAQ 633445). Photograph and line drawing of transverse section through an originally 4-locular fruit, showing the woody fruit wall (FW) which consists of two layers, an outer layer consisting of radially oriented sclereids, and an inner layer of tangentially oriented fibres; conspicuous foramina (F) extend through the wall, two ovules have developed into seeds (O), while two aborted and have been compressed and are represented by narrow spaces between adjoining locules, carpel walls (CW) form two parallel layers in the centre of the fruit, the seeds are large consisting of endosperm and developing embryo (E), fill the entire inside of the fruit, and they have a thin membranous seed coat (SC). 3–6. *Fontainocarpa foraminata*. 3.4. Line drawing and photograph of a partially mature, 5-locular fruit (QMF58787) highlighting the thick woody fruit wall (FW), conspicuous foramina (F) extend through the wall, three ovules (O) which have developed, and two have aborted, and the locules have been compressed and are represented by hollow spaces (L), there is no evidence of carpel walls. The ovules (O) are conspicuous and the seed coat is clearly evident with ventral vascular traces (VVT) positioned on the inner (ventral) side of each seed and two of the seeds have a coarsely crystalline quartz core with adhering siliceous matrix (M) on the outside of the fruit. The sutures (S) are clearly evident as both external and internal features in the fruit, and the intersutural surface (IS) between the sutures is concave in appearance. 5. 6. Photograph and line drawing of uniovulate fruit (QMF58788), showing the thick woody fruit wall in an originally 5-merous fruit, with four sutures evident, and one ovule (O) has developed, and four have aborted, and the young seed (O) occupies a large proportion of the inside of the fruit. The ventral position of the ventral trace (VT) is consistent with it being a ventral vascular trace of one of the ovaries. Scale bar = 5 mm. (see on page 48)

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